Research in adaptations of arthropods in British Columbia

RICHARD A. RING

BIOLOGY DEPARTMENT, UNIVERSITY OF VICTORIA, VICTORIA, BC, CANADA V8W 3N5

One of the major problems in reviewing this topic is defining the term adaptation. Unfortunately, biologists have often used the word adaptation to mean various, quite different things. However, for the purpose of this paper I will use the definition accepted by the majority of modern ecologists i.e. an adaptation is any morphological, physiological, sensory, developmental or behavioural character that enhances survival and reproduction success of an organism (Lincoln *et al.* 1998). This subject matter was not covered in any of the review papers of Volume 48 of the Journal in 1951 (50 years of entomology in BC), so I will take it upon myself to cover the last 100 years of research on arthropod adaptations in BC – not that there is much to report from before the 1960s! Since many aspects of adaptation research are likely to be covered in the other invited contributions to this issue, for example in forest entomology, insect population ecology, behavioural and chemical ecology, etc. I will concentrate my efforts in the field of eco-physiology which is, after all, the closest to my primary area of research. The paper will include not only work **done by** BC entomologists but also work **done on** BC insects by BC and other entomologists, and it will be written in chronological order, as far as is possible.

The earliest contribution that I can find that pertains to eco-physiological adaptations in insects of BC is the brief communication from Cockle (1917), where he explains some of the behavioural adaptations of "snow fleas" (Mecoptera; *Boreus californicus*) and five species of spiders to alpine conditions in the Kaslo area. In particular, he observed active feeding behaviour at temperatures down to between -2^0 and -3^0 C. From there we jump 22 years to Gregson (1939) who, in another brief paper, describes some of the adaptive features of that most Canadian of all insects, *Grylloblatta campodeiformis*. In the Kamploops area, these grylloblattids appear on the surface of rocky ground at relatively low altitudes (430-820 m) after the first frosts in November. They are active all winter, feeding on hibernating moths, ladybugs, wasps, bugs and spiders and even on active thysanurans and collembollans (in captivity they can be fed cockroaches!). They only appear on the surface at or around 0^0C. Above and below this temperature they seek shelter in rock crevices, as they do also during summer and other warmer months of the year. Their optimal foraging temperature is, in fact, 3.7^0C with cold prostration setting in at -6.2^0C and heat prostration at 27.8^0C. They die very soon at room temperatures around 22^0C. Gregson thus demonstrated that these rock crawlers are adapted to a very narrow temperature range for their feeding and other activities.

In 1944, R.W. Salt, working out of the Dominion Entomological Laboratory (now Agriculture Canada) in Lethbridge, Alberta, studied the behavioural adaptations and tolerance to cold in the larvae and pupae of the warble fly, *Hypoderma lineatus*, a serious pest of cattle in BC and Alberta. Most of the experimental insects came from Kamloops, BC. He found that both larvae and pupae were what we now call "freezing intolerant" i.e. they avoid freezing by supercooling to low temperatures, in this case to between -20^0 and -24^0C, indicating that early–dropped warble grubs would be frozen and killed. However, his behavioural studies showed that early-dropped grubs were immature forms and incapable of reaching full maturity. Fully mature grubs were never observed to drop before the danger of cold weather was past. These findings had important implications for stockmen regarding whether or not to use early chemical sprays to control warble fly populations. R.W. Salt went on to become one of the "founding fathers" in the discipline of insect cryobiology, and, in 1961, published his paper on the "Principles of insect cold-hardiness" which remains the foundation in this field of study to the present day. Then follows a paper by Morgan (1952), published in the same volume as the 50^{th} anniversary volume of the Proceedings of the Entomological Society of BC (Vol. 48). He describes the effects of low winter temperatures on four species of orchard mites in the Okanagan and Kootenay valleys after the coldest winter on record in this region of Western Canada (-28^0 to –36^{0}C). His experimental protocol involved collecting winter eggs from the field and incubating them at temperatures above 0^{0}C. His results showed that mortality increased from 40% at -27^{0}C to 100% at -40^{0}C. A few years later, Downes (1956) investigated the effects of the longest period of drought in southern BC – a continuous period of 95 days in summer with not more than a trace of water – on the insects of southern Vancouver Island and the adjacent mainland, particularly on some Hemiptera and Lepidoptera. Most populations of insects declined, although aphids increased their activities on Garry oak – probably due to the decline in populations of hemerobiids, chrysopids, coccinellids and syrphids. The main problem, however, was the associated decline in insect food plant production. The paper goes on to explain the harmful effects of the combination of heat and desiccation stress, but populations of these insects recovered, more or less, within 3 years.

The late 1960s was a relatively active period, particularly in studies of adaptations in forest insect pests. These studies, like most of the others described in the paper, were aimed at elucidating the "inherent" adaptations of each species, that is the built–in ability of the insect to adapt to its environment over time – including responses to changes in the environment within its own life cycle. Ross (1966) examined the ability of the introduced European pine shoot moth (*Rhyacionia buoliana*) to survive low winter temperatures in the Vernon area, and demonstrated that overwintering larvae can survive -4^0 F (-20^{0}C) which would be sufficient to allow this exotic pest to survive winters in most parts of the Okanagan Valley. In the meantime, Nijholt (1967, 1969) was studying the depletion of fat deposits during the long 7-month hibernation period of adult beetles of *Trypodendron lineatum*, an ambrosia beetle. Although his studies of fats were quantitative rather than qualitative, he did provide insights into how fat reserves affect the vigour of populations of these beetles during hibernation and the subsequent flight period and brood establishment. At the same time, Dyer (1969, 1970) and Gray and Dyer (1972) were elucidating the adaptive processes involved in diapause, cold tolerance, flight muscle degeneration and behaviour in the overwintering survival of bark beetles, *Dendroctonus* spp. There was not much further activity in this area of research during the remainder of the 1970s, although VanderSar (1977) wrote a very brief account demonstrating the ability of spruce beetle larvae (*Pissodes strobi*) to overwinter successfully in Sitka spruce leaders in coastal BC (Port Renfrew, Vancouver Island). Across most of its range, *Pissodes strobi* normally overwinters in the duff at the base of host trees and is thus protected from low winter temperatures by an insulating blanket of snow. Later, Safranyik and Linton (1991, 1998) studied the adaptations to low overwintering temperatures of the mountain pine beetle, *Dendroctonus ponderosae*, and the pine engraver beetle, *Ips pini*, under both field (1991) and experimental conditions (1998). Mortality to winter cold is one of the main factors determining the distribution and abundance of mountain pine beetle in BC, and it has been shown that overwintering larvae can withstand short exposures to –38°C. However, during autumn and spring, larvae are very susceptible to extreme cold, so unseasonably low temperatures (lower than –26^{0}C) at these times of year can cause widespread mortality. Under these conditions, mountain pine beetle larvae as well as the pine engraver beetle can only survive extreme low winter temperatures at the base of trees or among the duff where they are protected by a blanket of snow. In 1998, Li and Otvos, in attempting to provide a plentiful laboratory supply of western spruce budworm pupae (*Choristoneura occidentalis*) for research, reported their findings on adaptations to cold. Normally, western spruce budworm overwinters in obligatory diapause in the second larval instar in the field. However, a non-diapausing colony of this species can be induced in the laboratory and reared on an artificial diet. This has certain advantages for mass-rearing of a species for research purposes, and perhaps, for cold storage of beneficial biocontrol agents. Their results indicated that western spruce budworm pupae could be stored at low temperatures (2^0C) for up to 1 week without deterioration in subsequent adult quality.

Similar motives were involved in the work of Gillespie and Ramey (1988) and Morewood (1992a). Based on Morgan's (1952) work, these authors studied the cold hardiness and the cold storage potential of predatory mites (*Amblyseius cucumeris* and *Phytoseiulus persimilis*) as biocontrol agents that could be used as the controls for phytophagous mites and the western flower thrips, *Frankliniella occidentalis*. Gillespie and Ramey (1988) were able to show that *A. cucumeris* could survive at 9^0C for 10 weeks (63% survival) whereas only 1.2% survived 10 weeks at 2^0C. Similarly, Morewood's (1992b) techniques showed that although both species could survive short periods (e.g. 30 min) at -12.5^0C, all individuals died within 75 min of exposure to that temperature. He also calculated that under cold storage conditions, *A. cucumeris* could survive 2-3 weeks at 7.5^0C (the optimal temperature) whereas *P. persimilis* could survive 4-6 weeks under the same conditions. Gilkeson (1990) also worked on the problem of cold storage with the predatory midge, *Aphidoletes aphidimyza*, an important insect predator of aphids in greenhouses. The main aim of her cold storage program was to facilitate the balance between supply and demand in the biocontrol agent market.

The contributions from my laboratory at the University of Victoria have made many important advances in the field of insect cold-hardiness and eco-physiology (environmental physiology) in the last 20 years or so. With my graduate students and co-workers, we have attracted two international symposia on insect cold tolerance to the University of Victoria (in 1985 and 2000), the annual meeting of the Society for Cryobiology (1980) (where there was a special section on this topic), and a session at the International Congress of Entomology in Vancouver (1988). Most of this work is in the area of adaptations to low temperatures and desiccation resistance. Although many of these studies were conducted in the Canadian Arctic, some include insects from BC, such as the thimbleberry gall wasp (*Diastrophus kincaidi*) (Ring 1981), a willow leaf-gall sawfly (*Pontania* sp.) (Ring 1981), the cabbage-root maggot (*Delia radicum*) (Turnock *et al.* 1998), a pythid xylophagous beetle from high altitudes (*Pytho deplanatus*) (Ring 1981), the introduced European winter moth (*Operophtera brumata*), (Hale 1989; Ring and Danks 1994, 1998), the aphid, *Myzus persicae* (O'Doherty and Ring 1987) and several indigenous species of intertidal insects (Morley and Ring 1972; Parkinson and Ring 1983; Topp and Ring 1988a and 1988b; Ring 1989). During this time, I was also a collaborator in a comparative study carried out on the sub-antarctic island of South Georgia with the British Antarctic Survey, studying the adaptations of two endemic perimylopid beetles (*Perimylops antarcticus* and *Hydromedion sparsutum*) to low winter temperatures and relatively short summer growing seasons (Block *et al.* 1988; Ring *et al.* 1990).

Some of the major contributions from my laboratory have been: (1) identification of a multi-component cryoprotective system in the successful overwintering of insects, including a combination of glycerol, trehalose and sorbital (Ring 1977; Ring and Tesar 1980, 1981); (2) the discovery of the lowest supercooling point ever recorded for an insect, *Pytho americanus*, in the Western Canadian Arctic (Inuvik) at -61^oC; and (3) identification of the various anomalies that exist in northern insects, such as not only being freezing tolerant but also having a very low supercooling point (Ring 1982a). There are several other anomalies awaiting elucidation, such as the winter survival in the arctic of coccinellid beetles, which, apparently, lack any known cryoprotectant molecules (Ring 1982b). Humble (1987) made an important attempt to tease apart the co-evolutionary problems of cold versus desiccation tolerance and/or resistance. In arctic sawflies, he demonstrated that their abilities to survive low winter temperature and desiccation stress are co-adapted, that is, they are overlapping adaptations (see also Ring and Danks 1994, 1998). Similarly, Morewood (1999) studied the life history strategies and temperature versus development relationships of the high arctic woolly bear caterpillars (*Gynaephora* spp.) and their parasitoids at Alexandra Fiord, Ellesmere Island, Nunavut. Other contributions made in my laboratory towards an understanding of the adaptations of insects to the extreme temperature conditions of the arctic were by Winchester (1984) on arctic trichopteran larvae of the Tuktoyaktuk Peninsula in the western arctic, by Humble and Ring (1985) and Humble (1987) who studied the overwintering behaviour and adaptations of arctic willow sawflies and their parasitoids, and by DeBruyn and Ring (1999) on the overwintering behaviour and habitats of two species of diving beetles, *Hydroporus* spp. (Dytiscidae) in ponds at Alexandra Fiord, Ellesmere Island.

In the miscellaneous category, we find contributions from a variety of sources. At the top of the list I place G.G.E. Scudder, University of British Columbia (who has made three other contributions to this volume) and his collaborators who have made many insights into the ecological adaptations of water boatmen (Corixidae) that have successfully inhabited the saline lakes of Interior BC (Scudder 1976). With his students, he recognizes that many insects can, indeed, overcome the osmotic problems associated with these highly saline lakes – many of which are more saline than the sea – once again giving rise to that perennial entomological question “why have insects not re-invaded the sea?” Certainly not for the lack of osmoregulatory adaptations, according to this research. At the same time at UBC, J. Phillips and P. Hochachka were working on “pure” insect physiology. Nevertheless, much of their research also contributed knowledge towards our understanding of insect adaptations in the area of eco-physiology (see Hochachka and Somero 1973; Phillips 1975).

Ring (1978) studied the adaptive significance of spiracular gills in the pupae of the intertidal crane fly, *Limonia marmorata* (Tipulidae) (Fig. 1). This is a spectacular morphological adaptation which allows the pupae to respire both above and below water – an obvious advantage for any insect that lives in the intertidal zone. Other work that has taken place in the Ring laboratory on insect adaptations to the intertidal habitat is that of Morley and Ring (1972) on life history characteristics of intertidal chironomids, Parkinson and Ring (1983) on the osmoregulatory adaptations of these marine chironomids, and Topp and Ring (1988a, 1988b) on the adaptations of staphylinid beetles to both rocky shores and sandy beaches of the marine environment (Fig. 2). There then follows a paper (Ring 1991) that deals with insects that live in the natural hot springs of Hotspring Island, BC. These insects not only have to deal with wide temperature fluctuations but also with the associated osmoregulatory problems – the water of these natural springs is 2.5 times more saline than the sea. The chironomid midge larvae (*Thalassosmittia pacifica*) survive by being osmotic regulators in the surrounding medium rather than osmotic conformers. Other adaptations of marine chironomid larvae involve the up-take of dissolved organic nutrients from the surrounding seawater (Ring 1989). This is probably one of the least resolved but yet most intriguing questions in marine invertebrate zoology. My research has shown that these intertidal chironomids can utilize dissolved organic nutrients such as glucose, amino acids, etc. to enhance their nutrition. This is done by absorption through the cuticle of specialized areas in the intersegmental membranes of the larvae. This phenomenon may be more widespread among arthropods than was formerly recognized (see Chapman 1981).

Figure 1. Morphological adaptation – the spiracular gills of the pupa of the intertidal tipulid, *Limonia marmorata*. This structure allows the pupa to respire both above the water (low tide) and below the water level (high tide).

Figure 2. A typical view of the rocky intertidal zone on the west coast of British Columbia. Many insects exploit this habitat and show a whole suite of adaptations for survival in this extreme, inhospitable environment.

Another unexpected but interesting structural adaptation found among herbivorous insects going about their daily lives of eating plants, is the fact that many of them (if not all) incorporate metals into their already sclerotized mouthparts (mandibles) and claws. A good example of this can be found in Fontaine *et al.* (1991) where they demonstrated that zinc is prominent in the mandibles and claws of the mountain pine beetle (*D. ponderosae*), beetles which tunnel through bark as adults and as larvae mine tissues of the inner bark. Similar results were obtained from several species of coneworms (Lepidoptera: Pyralidae) where larvae mine cones and feed on developing seeds – all plant structures which have developed considerable toughness.

In summary, this paper provides, to the best of my knowledge, an up-date on the last 100 years of research in the adaptations of arthropods (mainly insects) in BC. It chronicles those papers dealing with various aspects of eco-physiology, but also includes work carried out on morphological/structural and behavioural characteristics. About one-third of the papers have been published in the Journal (or Proceedings) of the Entomological Society of BC. Please excuse me, reader, if I have not included your seminal work in this article!

REFERENCES

Block, W., L. Somme, R.A. Ring, P. Ottesen and M.R. Worland. 1988. Adaptations of arthropods to the sub-antarctic environment. British Antarctic Survey Bulletin 81: 65-67.

Chapman, P.M. 1981. Evidence for dissolved glucose uptake from seawater by *Neocalanus plumchrus* (Arthropoda, Copepoda). Canadian Journal of Zoology 59: 1618-1621.

Cockle, J.W.M. 1917. Notes on the hybernation of some larvae and the movement of *Boreus* in the snow. Proceedings of the Entomological Society of British Columbia 10: 14-15.

DeBruyn, A.M.H. and R.A. Ring. 1999. Comparative ecology of two species of *Hydroporus* (Coleoptera: Dytiscidae) in a high arctic oasis. The Canadian Entomologist 131: 405-420.

Downes, W. 1956. Observations on the effect of drought in insect populations with special reference to Heteroptera, Homoptera and Lepidoptera. Proceedings of the Entomological Society of British Columbia 52: 12-16.

Dyer, E.D.A. 1969. Influence of temperature inversion on development of spruce beetle, Dendroctonus obesus (Mannerheim) (Coleoptera: Scolytidae). Journal of the Entomological Society of British Columbia 66: 41-45.

Dyer, E.D.A. 1970. Larval diapause in *Dendroctonus obesus* (Mannerheim) (Coleoptera:Scolytidae). Journal of the Entomological Society of British Columbia 69: 41-43.

Fontaine, A.R., N. Olsen, R.A. Ring and C.L. Singla. 1991. Cuticular metal hardening of mouthparts and claws of some forest insects of British Columbia. Journal of the Entomological Society of British Columbia 88: 45-55.

Gilkeson, L. 1990. Cold storage of the predatory midge *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae). Journal of Economic Entomology 83: 965-970.

Gillespie, D.G. and C.A. Ramey. 1988. Life history and cold storage of *Amblyseius cucumeris* (Acarina: Phytoseiidae). Journal of the Entomological Society of British Columbia 85: 71-76.

Gray, T.G. and E.D.A. Dyer. 1972. Flight-muscle degeneration in spruce beetles, *Dendroctonus refipennis* (Coleoptera: Scolytidae). Journal of the Entomological Society of British Columbia 69: 41-43.

Gregson, J.D. 1939. Notes on the occurrence of *Grylloblatta campodeiformis* Walker in the Kamloops District. Proceedings of the Entomological Society of British Columbia 35: 29-30.

Hale, M.A. 1989. Factors affecting the distribution and survival of an endemic and an introduced species of *Operophtera* (Lepidoptera: Geometridae). M.Sc. Thesis, University of Victoria, Victoria, BC. 90pp.

Hochachka, P.W. and G.N. Somero. 1973. Strategies of Biochemical Adaptation.Saunders, Philadelphia.

Humble, L.M. 1987. Life histories and overwintering strategies of some arctic sawflies and their hymenopterous parasitoids. Ph.D. Thesis, University of Victoria, Victoria, BC. 340 pp.

Humble, L.M. and R.A. Ring. 1985. Inoculation freezing of a larval parasitoid within its host. Cryo-Letters 6: 59-66.

Li, S.Y. and I.S. Otvos. 1998. Effects of cold storage on adult emergence and fecundity of *Choristoneura occidentalis* (Lepidoptera: Tortricidae). Journal of the Entomological Society of British Columbia 95: 3-7.

Lincoln, R., G. Boxshall and P. Clark. 1998. A Dictionary of Ecology, Evolution and Systematics. 2nd ed. Cambridge University Press, Cambridge, UK. 361pp.

Morewood, W.D. 1992a. Cold hardiness of *Phytoseiulus persimilis* Athias-Henriot and *Amblyseius cucumeris* (Oudemans) (Acarina: Phytoseiidae). The Canadian Entomologist124: 1015-1025.

Morewood, W.D. 1992b. Cold hardiness and cold storage of *Phytoseiulus persimilis* and *Amblyseius cucumeris* (Acarina: Phytoseiidae). M.Sc. Thesis, University of Victoria, Victoria, BC. 63pp.

Morewood, W.D. 1999. Temperature/development relationships and life history strategies of arctic *Gynaephora* species (Lepidoptera: Lymantriidae) and their insect parasitoids (Hymenoptera: Ichneumonidae and Diptera: Tachinidae), with reference to predicted global warming. Ph.D. Thesis, University of Victoria, Victoria, BC. 340pp.

Morgan, C.V.G. 1952. Effects of low winter temperatures on some orchard mites. Proceedings of the Entomological Society British Columbia 48: 90-93.

Morley, R.L. and R.A. Ring. 1972. The intertidal Chironomidae (Diptera) of British Columbia. II. Life History and population dynamics. The Canadian Entomologist 104: 1099-1121.

Nijholt, W.W. 1967. Moisture and fat content during the adult life of the Ambrosia beetle, *Trypodendron lineatum* (Oliv.). Journal of the Entomological Society of British Columbia 64: 51-55.

Nijholt, W.W. 1969. Fat content of the ambrosia beetle, *Trypodendron lineatum* (Oliv.)during attack and brood production. Journal of the Entomological Society of British Columbia 66: 29-31.

O'Doherty, R. and R.A. Ring. 1987. Super coding ability of aphid populations from British Columbia and the Canadian Arctic. Canadian Journal of Zoology 65: 763-765.

Parkinson, A. and R.A. Ring. 1983. Osmoregulation and respiration in a marine chironomid larva, *Paraclunio alaskensis* Coquillett (Diptera, Chironomidae). Canadian Journal of Zoology 61: 1937-1943.

Phillips, J.E. 1975. Environmental Physiology. Wiley, New York.

Ring, R.A. 1977. Cold hardiness of the bark beetle, *Scolytus ratzeburgi* (Coleoptera, Scolytidae). Norwegian Journal of Entomology 24: 125-136.

Ring, R.A. 1978. Spiracular gills of the pupa of the intertidal crane fly, *Limonia* (*Idioglochina*) *marmorata* (Diptera: Tipulidae). The Canadian Entomologist 110: 1277-1280.

Ring, R.A. 1981. The physiology and biochemistry of cold tolerance in arctic insects.Journal of Thermal Biology 6: 219-229.

Ring, R.A. 1982a. Freezing-tolerant insects with low supercooling points. Comparative Biochemistry and Physiology 73A: 605-612.

Ring, R.A. 1982b. Freezing tolerance and intolerance: variations within a theme. Cryo-Letters 3: 181-190.

Ring, R.A. 1989. Intertidal Chironomidae of B.C., Canada. Acta Biologica Oecologica Hungaricae 3: 275-288.

Ring, R.A. 1991. The insect fauna and some other characteristics of natural salt springs on Saltspring Island, British Columbia. Memoirs of the Entomological Society of Canada. 155: 51-56.

Ring, R.A. and H.V. Danks. 1994. Desiccation and cryoprotection: overlapping adaptations. Cryo-Letters 15: 181-190.

Ring, R.A. and H.V. Danks. 1998. The role of trehalose in cold-hardiness and desiccation. Cryo-Letters 19: 275-282.

Ring, R.A. and D. Tesar. 1980. Cold hardiness of the arctic beetle, *Pytho americanus* Kirby Coleoptera, Pythidae (Salpingidae). Journal of Insect Physiology 26: 763-774.

Ring, R.A. and D. Tesar. 1981. Adaptations to cold in Canadian arctic insects. Cryobiology 18: 199-211.

Ring, R.A., W. Block, L. Somme and M. R. Worland. 1990. Body water content and desiccation resistance in some arthropods from sub-antarctic South Georgia. Polar Biology 10: 581-588.

Ross, D.A. 1966. Overwintering of caged *Rhyacionia buoliana* (Schiffermuller) at Vernon, B.C. in 1965-66. Journal of the Entomological Society of British Columbia 63: 31-32.

Safranyik, L. and D.A. Linton. 1991. Unseasonably low fall and winter temperatures affecting mountain pine beetle and pine engraver beetle populations and damage in the British Columbia Chilcotin Region. Journal of the Entomological Society of British Columbia 88: 17-21.

Safranyik, L. and D.A. Linton. 1998. Mortality of mountain pine beetle larvae, *Dendroctonus ponderosae* (Coleoptera: Scolytidae) in logs of lodgepole pine (*Pinus contorta* var *latifolia*) at constant low temperatures. Journal of the Entomological Society of British Columbia 95: 87-87.

Salt, R.W. 1944. The effects of subzero temperatures on *Hypoderma lineatum* DeVill. Canadian Journal of Agricultural Science 25: 156-160.

Salt, R.W. 1961. Principles of insect cold-hardiness. Annual Review of Entomology 6: 55-74.

Scudder, G.G.E. 1976. Water-boatmen of saline waters (Hemiptera: Corixidae). Pp. 263-289 In: L. Cheng (Ed.) Marine Insects. North Holland Publishing Company.

Topp, W. and R.A. Ring. 1988a. Adaptations of Coleoptera to the marine environment. I. Observations on rove beetles (Staphylinidae) from sandy beaches. Canadian Journal of Zoology 66: 2464-2468.

Topp, W. and R.A. Ring. 1988b. Adaptations of Coleoptera to the marine environment.II. Observations on rove beetles (Staphylinidae) from rocky shores. Canadian Journal of Zoology 66: 2469-2474.

Turnock, W.J., G. Boivin and R.A. Ring. 1998. Inter-population differences in the cold-hardiness of *Delia radicum* (L.) (Diptera: Anthomyiidae) The Canadian Entomologist 130: 119-129.

VanderSar, T.J.D. 1977. Overwintering survival of *Pissodes strobi* (Peck) (Coleoptera: Curculionidae) in Sitka spruce leaders. Journal of the Entomological Society of British Columbia 74: 37.

Winchester, N.N. 1984. Life histories and post-glacial origins of tundra caddisflies (Trichoptera) from the Tuktoyaktuk Peninsula, Northwest Territories. M.Sc. Thesis, University of Victoria, Victoria, BC. 299pp.